

WATER VAPOUR FLUX IN THE EGGS OF TWO SPECIES OF RAIL (RALLIDAE) DURING INCUBATION

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Swamp-dwelling purple swamphens and dusky moorhens lay their eggs in shallow, open nests, typically built of reeds, placed a few centimetres above water level and consequently sometimes noticeably damp. Nest humidity and egg water vapour flux parameters were measured to determine the extent to which the eggs of these species have a water balance problem during incubation. Mean water vapour pressures in the nest were comparatively high (3.6-3.7 kPa). Calculated incubation temperatures averaged 36-37°C and consequently the water vapour pressure gradient across the eggshell was fairly shallow (2.5-2.6 kPa); however, these values were not sufficient to cause a significant water flux problem in the egg. The egg's mean rate of water loss (185-188 mg.day⁻¹), fractional mass loss during incubation (12-13%), water vapour conductance (71.43-74.36 mg (day.kPa)⁻¹) and total functional pore area (1.04-1.15 mm²) all conformed with allometric predictions based on the ratio of egg mass:incubation period. Despite their nest placement and nesting habits, the two species do not exhibit the wet-nesting syndrome typical of some freshwater birds such as grebes and loons.

MOST bird eggs lose 12-18% of their initial mass as water vapour during the incubation period, mainly by diffusion through microscopic pores in the shell. This is crucial in promoting optimal hatching success. The rate of water loss is determined by the water vapour pressure difference across the shell (ΔP_{H_2O}) and its water vapour conductance (G_{H_2O} , in mg (day.kPa)⁻¹). G_{H_2O} is governed by the number, size and length of the pores (Ar & Rahn 1980). Although this gas flux system is now well understood, ecologically-induced, atypical patterns of egg water content regulation remain of great interest.

Water vapour pressure in the nest (P_n) of birds breeding in a wide variety of conditions averages about 2.7 kPa (Walsberg 1980), but the nest microclimate of some grebes (Podicipedidae), loons (Gaviidae) and megapodes (Megapodiidae) is significantly more humid (Seymour & Rahn 1978, Sotherland et al. 1984, Ar & Rahn 1985). Nonetheless, the eggs of these so-called "wet-nesters" maintain an optimal state of hydration during incubation through having such features as a plastron-like outer shell structure resistant to liquid water influx (Board 1982, Sotherland et al. 1984), or a greatly elevated G_{H_2O} (Ar & Rahn 1985). However, the extent and causes of the wet-nesting syndrome, and

variations in this phenomenon, are still poorly documented.

In eastern Australia, the dusky moorhen, *Galimula tenebrosa*, and purple swamphen, *Porphyrio porphyrio*, commonly nest in dense reed beds in the same wetlands. Their nests are shallow bowls, made of reeds and rushes (although moorhens sometimes use twigs and bark) and often placed only a few centimetres above water level (Beruldsen 1980). Some nests are noticeably damp at times due to short-term water level fluctuations, condensation "run-off" from the dense surrounding vegetation and from moisture transported on the incubating adults' body. Both species are therefore potentially wet-nesters. This investigation examined whether the microclimate of moorhen and swamphen nests is unusually humid and, if so, whether this generates any water balance problem in the egg.

METHODS

Field data were obtained from September-December in several years from 7 locations within 150 km of Melbourne, including Healesville, Coldstream, Werribee and Heidelberg. During these months, Melbourne has an average relative humidity of 60-68% and average daily maximal and minimal temperatures of about

17–25°C and 6–14°C respectively. Eggs were collected under permit from four of the sites for experimental work. Nesting habitat comprised artificial and natural ponds, dams, lakes and marshes, often with emergent stands of *Typha* sp. and *Eleocharis* sp.

The initial mass of eggs (± 0.01 g) was determined: (a) by weighing newly-laid eggs in the field on a wind-shielded Shinko Denshi portable balance, and (b) for a further sample of partly developed eggs, by estimation from their linear dimensions (± 0.05 mm), using the equation

$$W = K_w \times LB_{\max}^2 \text{ (Hoyt 1979),}$$

where W is fresh mass (g), L is length, B_{\max} is maximum breadth (mm) and K_w is a species-typical constant which was empirically determined for both species.

The mean daily mass loss of incubated eggs at various stages of development was determined by marking them with indelible ink and weighing them (as above) at intervals of 5–22 days. Since nearly all mass loss can be attributed to water vapour loss (Drent 1970, Rahn & Ar 1974), this value equals the mean daily rate of water loss (M_{H_2O} , in $\text{mg}\cdot\text{day}^{-1}$).

Nest humidity was determined by the method of Rahn et al. (1977a). The gain in mass of hygrometer eggs (consisting of eggshells fitted with metal screw caps and filled with dry silica gel) when placed in active nests for periods of 2–4 days was divided by their water vapour conductance. The latter quantity was determined by measuring their mean daily mass gain at 20°C and 76% RH in the laboratory over a 4 day period.

G_{H_2O} of intact eggs was determined by the method of Ar et al. (1974). The daily weight loss (± 1 mg) of eggs placed over dry silica gel in a desiccator at 20°C was measured over 8–9 days. Values obtained were corrected to a barometric pressure of 101.33 kPa and also to a temperature of 25°C to facilitate interspecific comparisons. Determinations were mostly done on fresh eggs, but a few older eggs were included to give an indication of whether shell conductance increased markedly during incubation, as reported for a few bird species (Carey 1979).

Shell parameters influencing the egg's G_{H_2O} were measured on dried shells which were cut with a dental drill with a cutting bit into equatorial, pointed and blunt pole sections. True shell thickness (L) and pore density were measured on 12 equatorial and 6 polar (3 from each pole) fragments from each egg. The fragments were first briefly boiled in 5% NaOH to remove the shell membranes. L (± 1 μm) was measured with a

Tesa dial micrometer fitted with an hemispherical anvil to accommodate the curvature of the shell. Pore density was determined for the same fragments by painting the inner surface with acid fuchsin, which penetrated the pores so that they could be detected as discrete spots on the outer surface (Ar & Rahn 1985). The fragments were mounted on a Nikon V20A Profile Projector and the number of pores in a 25 mm^2 area counted from the magnified ($\times 20$) image. For each species, the number of pores in an egg of average size (N) was calculated as the product of mean pore density and surface area, which was estimated from equation (12) of Hoyt (1976). Pore shape and form were examined by viewing platinum-coated, radial sections of shell under an Hitachi S570 SEM.

The relative magnitude of egg water vapour flux parameters in swamphens and moorhens was assessed by comparing observed values with those predicted from egg mass/incubation period (M/I) (relative embryonic growth rate) using established regression equations based on data for many species (sources in Table 1).

RESULTS

Egg size measurements and mean values for egg parameters which influence its water vapour flux are summarised for both species in Table 1.

In the purple swamphen, P_n averaged 3.7 \pm 0.4 kPa (range 2.9–4.1 kPa; $n = 16$ determinations for 10 nests); only three values were less than 3.5 kPa. 36.3 g, the average of the two estimates derived respectively by weighing and from dimensions, was taken as the best estimate of mean initial egg mass. At the mean M_{H_2O} observed, an egg of this mass would have an estimated fractional mass loss of c. 12% over the 24 day incubation period. G_{H_2O} corrected to 25°C ranged from 60.23 to 102.63 $\text{mg}\cdot(\text{day}\cdot\text{kPa})^{-1}$; the mean values for the three older eggs and the nine fresh eggs, which had equivalent mean initial masses, were not significantly different (75.65 ± 12.61 versus 70.60 ± 11.24 $\text{mg}\cdot(\text{day}\cdot\text{kPa})^{-1}$; $t_{(10)} = 0.613$, $p > 0.05$). The mean ΔP_{H_2O} in the nest was 2.5 kPa. The mean saturated vapour pressure of the egg contents was therefore 6.1 kPa, which translates into a mean incubation temperature of 36–37°C. Pore density averaged 28 ± 10 , 25 ± 8 and 35 ± 8 pores per 25 mm^2 at the pointed pole, equator and blunt pole respectively.

In the dusky moorhen, P_n averaged 3.6 \pm 0.4 kPa (range 2.9–4.2 kPa; $n = 11$ determinations

Parameter	Swamphen		Moorhen	
	Observed mean	Ratio observed: predicted means	Observed mean	Ratio observed: predicted means
Length (mm)	52.12 ± 2.19 (53;16)		50.55 ± 2.49 (20;6)	
Max. breadth (mm)	36.41 ± 0.91 (53;16)		35.03 ± 1.52 (23;8)	
Initial mass (g)	35.14 ± 3.25 (31;13)		33.42 ± 2.89 (21;7)	
Estimated initial mass (g)	37.45 ± 2.80 (45;10)		33.82 ± 4.39 (14;4)	
I (days)	24		24	
M _{H₂O} (mg.day ⁻¹)	185 ± 38 (61;13)	0.83	188 ± 35 (136;16)	0.91
G _{H₂O} (mg.[day.kPa] ⁻¹)	74.36 ± 12.03 (12;11)	1.30	71.43 ± 16.09 (15;12)	1.35
L (µm)	235 (20;15)	0.85	270 (12;10)	1.02
N	6087 (20;15)	1.18	5132 (12;10)	1.07
A _p (mm ²) ^a	1.04	1.33	1.15	1.38

^a "observed" value calculated from measured G_{H₂O} and L

Table 1. Size and water vapour flux parameters of rail eggs. Numbers in parentheses are sample sizes of (eggs; nests). I = incubation period; M_{H₂O} = daily rate of water loss; G_{H₂O} = water vapour conductance; L = shell thickness; N = pores per egg; A_p = total effective pore area. Mean K_w used to obtain initial egg mass estimate was 0.541 (swamphen) and 0.539 (moorhen). Estimates of I based on personal observations and on Falla et al. (1985), Garnett (1978), O'Grady & Lindsey (1979), National Photographie Index (1985) and Williams (1966). Sources for predictions: M_{H₂O}, Ar & Rahn (1980); G_{H₂O}, L and N, Ar & Rahn (1985); A_p, Ar & Rahn (1978); predictions based on egg mass/incubation period.

for 6 nests); only three values were less than 3.5 kPa. Mean initial egg mass, derived as for the swamphen, was 33.6 g. At the mean M_{H₂O} recorded, an egg of this mass would have a fractional mass loss of about 13% over the 24 day incubation period. G_{H₂O} corrected to 25°C ranged from 46.24 to 107.02 mg.(day.kPa)⁻¹; the mean conductances of three older eggs with an average initial mass of 32.3 g and nine fresh eggs with an average mass of 34.9 g did not differ significantly (77.67 ± 9.02 versus 69.25 ± 20.08 mg.(day.kPa)⁻¹; *t*₍₁₀₎ = 0.686, *p* > 0.05). ΔP_{H₂O} was calculated to be 2.6 kPa and the mean saturated vapour pressure of the egg contents was therefore estimated to be 6.2 kPa, which translates into a mean incubation temperature of 36–37°C. Pore density of the shell averaged 26 ± 8, 25 ± 6 and 31 ± 8 pores per 25 mm² at the pointed pole, equator and blunt pole respectively. Pores were unbranched, had open orifices and were mostly posthorn-shaped.

DISCUSSION

Given the prevailing ambient temperatures and relative humidities in the study region (see Methods), mean water vapour pressure in the nests of both rails must have been substantially above environmental levels. The calculated mean saturated vapour pressure of the egg contents of the two species was similar to that reported for many other bird species (Walsberg 1980, Rahn 1984) and translates into a mean incubation temperature which is fairly typical of

many birds that maintain a high incubation constancy (Drent 1972). Mean P_n in both species was substantially higher than the averages reported for a large sample of bird species breeding in a variety of environments (2.0–2.8 kPa; Rahn et al. 1977a, Ar & Rahn 1978, Walsberg 1980, Rahn 1984). Mean ΔP_{H₂O} was substantially smaller than the mean values calculated for many other bird species nesting in various environments (3.6–4.7 kPa; Rahn & Ar 1974, Rahn et al. 1977b, Ar & Rahn 1978, 1980, Walsberg 1980, Rahn 1984).

However, P_n and ΔP_{H₂O} were clearly not so unusual as to necessitate any significant compensatory changes in G_{H₂O} or the shell parameters that influence it. Mean values obtained for these factors all lie within the 95% confidence limits of the values predicted by the allometric equations referred to in Table 1. In acknowledged wet-nesters, such as grebes and brush turkeys, where P_n is much higher (4.3–6.4 kPa) and ΔP_{H₂O} much smaller than in the rails, G_{H₂O} and N usually exceed allometrically predicted values by more than two standard errors of estimate (Seymour & Rahn 1978, Davis et al. 1984, Ar & Rahn 1985). This contrast clearly occurs because the eggs of grebes and brush turkeys, unlike those of swamphens and moorhens, are permanently or intermittently covered by warm, moist vegetation, and the eggs of grebes are also often in contact with liquid water.

Comparative data on egg water vapour flux for other rail species are few. M_{H₂O} and N are as expected from egg mass in the king rail, *Rallus*

elegans, and grey moorhen, *Gallinula chloropus*, respectively (Meanly 1969, Ar & Rahn 1985). However, M_{H_2O} is significantly (30–31%) lower than expected in the Sora rail, *Porzana carolina* (Drent 1970), and G_{H_2O} is 87% greater than would be predicted from egg mass in the Eurasian coot, *Fulica atra* (Lomholt 1976). In the American coot, *Fulica americana*, P_n is not particularly elevated (2.4 kPa) and G_{H_2O} accords with allometric predictions; the egg has a standard fractional mass loss during incubation, yet M_{H_2O} is 17–21% less than would be expected on allometric grounds (Drent 1970, Davis et al. 1984).

Much more work is required before the incidence of wet-nesting in the Rallidae can be fully assessed. Clearly, however, the purple swamphen and dusky moorhen, despite their nesting habits, do not exhibit the wet-nesting syndrome typical of some other freshwater birds with similar nest placement, such as grebes and loons.

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